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## A MENDELIAN INTERPRETATION OF VARIATION THAT IS APPARENTLY CONTINUOUS<sup>1</sup>

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THERE are two objects in writing this paper. One is to present some new facts of inheritance obtained from pedigree cultures of maize; the other is to discuss the hypotheses to which an extension of this class of facts naturally leads. This discussion is to be regarded simply as a suggestion toward a working hypothesis, for the facts are not sufficient to support a theory. They do, however, impose certain limitations upon speculation which should receive careful consideration.

The facts which are submitted have to do with independent allelomorphic pairs which cause the formation of like or similar characters in the zygote. Nilsson-Ehle<sup>2</sup> has just published facts of the same character obtained from cultures of oats and of wheat. My own work is largely supplementary to his, but it had been given these interpretations previous to the publication of his paper.

In brief, Nilsson-Ehle's results are as follows: He found that while in most varieties of oats with black

<sup>1</sup> Contributions from the Laboratory of Genetics, Bussey Institution, Harvard University, No. 4. Read before the annual meeting of the American Society of Naturalists, Boston, December 29, 1909.

<sup>2</sup> Nilsson-Ehle, H. Kreuzungsuntersuchungen an Hafer und Weizen. Lunds Universitets Årsskrift, N. F. Afd. 2., Bd. 5, No. 2, 1909.

glumes blackness behaved as a simple Mendelian monohybrid, yet in one case there were two definite independent Mendelian unit characters, each of which was allelomorphic to its absence. Furthermore, in most varieties of oats having a ligule, the character behaved as a monohybrid dominant to absence of ligule, but in one case no less than four independent characters for presence of ligule, each being dominant to its absence, were found. In wheat a similar phenomenon occurred. Many crosses were made between varieties having red seeds and those having white seeds. In every case but one the  $F_2$  generation gave the ordinary ratio of three red to one white. In the one exception—a very old red variety from the north of Sweden—the ratio in the  $F_2$  generation was 63 red to 1 white. The reds of the  $F_2$  generation gave in the  $F_3$  generation a very close approximation to the theoretical expectation, which is 37 constant red, 8 red and white separating in the ratio of 63:1, 12 red and white separating in the ratio of 15:1, 6 red and white separating in the ratio of 3:1, and one constant white. He did not happen to obtain the expected constant white, but in the total progeny of 78  $F_2$  plants his other results are so close to the theoretical calculation that they quite convince one that he was really dealing with three indistinguishable but independent red characters, each allelomorphic to its absence. Nor can the experimental proof of the two colors of the oat glumes be doubted. The evidence of four characters for presence of ligule in the oat is not so conclusive.

In my own work there is sufficient proof to show that in certain cases the endosperm of maize contains two indistinguishable, independent yellow colors, although in most yellow races only one color is present. There is also some evidence that there are three and possibly four independent red colors in the pericarp, and two colors in the aleurone cells. The colors in the aleurone cells when pure are easily distinguished, but when they are together they grade into each other very gradually.

Fully fifteen different yellow varieties of maize have been crossed with various white varieties, in which the crosses have all given a simple mono-hybrid ratio. In the other cases that follow it is seen that there is a di-hybrid ratio.

No. 5-20, a pure white eight-rowed flint, was pollinated by No. 6, a dent pure for yellow endosperm. An eight-rowed ear was obtained containing 159 medium yellow kernels and 145 light yellow kernels. The pollen parent was evidently a hybrid homozygous for one yellow which we will call  $Y_1$  and heterozygous for another yellow  $Y_2$ . The gametes  $Y_1Y_2$  and  $Y_1$  fertilized the white in equal quantities, giving a ratio of approximately one medium yellow to one light yellow. The  $F_2$  kernels from the dark yellow were as follows:

TABLE I.<sup>3</sup>

$F_2$  SEEDS FROM CROSS OF NO. 5-20, WHITE FLINT  $\times$  NO. 6 YELLOW DENT,  
HOMOZYGOUS FOR  $Y_1$  AND HETEROZYGOUS FOR  $Y_2$

*Dark Seeds Heterozygous for Both Yellows Planted*

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.
1	270	56	326	29
2	101	215	316	27
3	261	52	313	28
5	273	284	557	35
10	358	117	475	25
12	296	72	368	19
13	207	156	363	35
14	387	102	489	29
Total	2153	1054	3207	227
Ratio			14.1	1

The ratios of light yellows to dark yellows is very arbitrary, for there was a fine gradation of shades. The ratio of total yellows to white, however, is unmistakably 15:1.

In the next table (Table II) are given the results of  $F_2$  kernels from the light yellows of  $F_1$ . Only ear No. 8, which was really planted with the dark yellows, showed yellows dark enough to be mistaken for kernels containing

<sup>3</sup> In these tables only hand pollinated ears are given.

both  $Y_1$  and  $Y_2$ . The remaining ears are clearly mono-hybrids with reference to yellow endosperm.

TABLE II.

$F_2$  SEEDS FROM SAME CROSS AS SHOWN IN TABLE I  
*Light Yellow Seeds Heterozygous for  $Y_1$  Planted*

Ear No.	Dark Y.	Light Y.	No Y.
1	331	359	117
2		144	54
3		173	63
4		433	136
6		316	120
8			109
8a		229	86
9		325	115
10		227	87
11 <sup>4</sup>		4	434
12		318	118
13		256	93
Total		3111	1098
Ratio		2.8	1

In a second case the female parent possessed the yellow endosperm. No. 11, a twelve-rowed yellow flint, was crossed with No. 8, a white dent. The  $F_2$  kernels in part showed clearly a mono-hybrid ratio, and in part blended gradually into white. Two of these indefinite ears proved in the  $F_3$  generation to have had the 15:1 ratio in the  $F_2$  generation. Ear 7 of the  $F_2$  generation calculated from the results of the entire  $F_3$  crop must have had about 547 yellow to 52 white kernels, the theoretical number being 561 to 31. The hand-pollinated ears of the  $F_3$  generation (yellow seeds) gave the results shown in Table III.

The  $F_3$  generation grown from the other ear, Ear No. 8, showed that the ratio of yellows to whites in the  $F_2$  generation was about 227 to 47. As the theoretical ratio is 257 to 17, the ratio obtained is somewhat inconclusive. A classification of the open field crop could not be made accurately on account of the light color of the yellows and

<sup>4</sup>Discarded from average. This ear evidently grew from one kernel of the original white mother that was accidentally self-pollinated. The four yellow kernels all show zenia from accidental pollination in the next generation.

TABLE III.

No. 11 YELLOW  $\times$  No. 8 WHITE $F_3$  Generation from Yellow Seeds of  $F_2$  Generation

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.	Ratio They Approximate.
1	116	95	211	19	15Y : 1 no Y
14			88	5	15Y : 1 no Y
5	181	122			3Y <sub>1</sub> Y <sub>2</sub> : 1 Y <sub>1 or 2</sub>
4		253		68	3Y : 1 no Y
6		193		73	"
8		163		79	"
11		108		35	"
9		456			Constant Y <sub>1 or 2</sub>

the presence of many kernels showing zenia. Table IV, however, showing the hand-pollinated kernels of the interbred yellows of the  $F_2$  generation, settles beyond a doubt the fact that the two yellows were present.

TABLE IV.

PROGENY OF EAR NO. 8 OF THE SAME CROSS AS SHOWN IN TABLE III

 $F_3$  Generation from Yellow Seeds of  $F_2$  Generation

Ear No.	Dark Y.	Light Y.	Total Y.	No Y.	Ratio They Approximate.
10	101	188	289	25	15Y : 1 no Y
11	89	219	308	23	15Y : 1 no Y
3		233			constant light Y
9	dark and light		331		3 dark : 1 light Y
13	dark and light		350		3 dark : 1 light Y
8		294		108	3 light : 1 no Y
15		221		87	3 light : 1 no Y
1 <sup>5</sup>		197		203	

In a third case an eight-rowed yellow flint, No. 22, was crossed with a white dent, No. 8. Only four selfed ears were obtained in the  $F_2$  generation. Ear 1 had 72 yellow to 37 white kernels. This ear was poorly developed and undoubtedly had some yellow kernels which were classed as whites. Ear 4 had 158 yellow and 42 white kernels. It is very likely that both of these ears were mono-hybrids, but the  $F_3$  generation was not grown. Ear 5 had 148 yellow and 15 white kernels. Ear 7 had 78 yellow and 5 white kernels. It seems probable that both of these ears

<sup>5</sup> Kernel from which this ear grew was evidently pollinated by no Y.

were di-hybrids, but only Ear 5 was grown another generation. The kernels classed as white proved to be pure; the open field crop from the yellow kernels gave 14 pure yellow ears and 14 hybrid yellow. Theoretically the ratio should be 7 pure yellows (that is, pure for either one or both yellows) and 8 hybrid yellows (4 giving 15 yellows to 1 white and 4 giving 3 yellows to 1 white). Five hand-pollinated selfed ears were obtained. Three of these gave mono-hybrid ratios, with a total of 607 yellows to 185 white kernels. One ear was a pure dark yellow (probably  $Y_1Y_1Y_2Y_2$ ). The other ear was poorly filled, but had 27 dark yellows (probably  $Y_1Y_2$ ) and 7 light yellow kernels ( $Y_1$  or  $Y_2$ ). Unfortunately no 15:1 ratio was obtained in this generation, but this is quite likely to happen when only five selfed ears are counted. The gradation of colors and the general appearance of the open field crop, however, lead me to believe that we were again dealing with a di-hybrid.

Two yellows appeared in still another case, that of white sweet No. 40 ♀  $\times$  yellow dent No. 3 ♂. Only one selfed ear was obtained in the  $F_2$  generation giving 599 yellow to 43 white kernels. Of these kernels 486 were starchy and 156 sweet, which complicated matters in the  $F_3$  generation because it was very difficult to separate the light yellow sweet from the white sweet kernels. Among the selfed ears were three pure to the starchy character, and in these ears the dark yellows, the light yellows and whites stood out very distinctly. Ear 12 had 156 dark yellow; 47 light yellow; 14 white kernels. Ear 13 had 347 dark yellow; 93 light yellow; 25 white kernels. The third starchy ear, No. 6, had 320 light yellow; 97 white kernels. Two ears, therefore, were di-hybrids, and one ear a mono-hybrid.

The ears which were heterozygous for starch and no starch and those homozygous for no starch, could not all be classified accurately, but it is certain that some pure dark yellows, some pure light yellows, some showing segregation of yellows and whites at the ratio 15:1, and some

showing segregation of yellows and whites at the ratio of 3:1, were obtained,

One other case should be mentioned. One ear of a dent variety of unknown parentage obtained for another purpose was found to have some apparently heterozygous yellow kernels. Seven selfed ears were obtained from them, of which two were pure yellow. The other five ears each gave the di-hybrid ratio. There was a total of 1906 yellow seeds to 181 white seeds, which is reasonably close to the expected ratio, 1956 yellow to 131 white.

It is to be regretted that I can present no other case of this class that has been fully worked out, although several other characters which I have under observation in both maize and tobacco seem likely to be included ultimately. Nevertheless, the fact that we have to deal with conditions of this kind in studying inheritance is established; granting only that they will be somewhat numerous, it opens up an entirely new outlook in the field of genetics.

In certain cases it would appear that we may have several allelomorphic pairs each of which is inherited independently of the others, and each of which is separately capable of forming the same character. When present in different numbers in different individuals, these units simply form quantitative differences. It may be objected that we do not know that two colors that appear the same physically are exactly the same chemically. That is true; but Nilsson-Ehle's case of several unit characters for presence of ligule in oats is certainly one where each of several Mendelian units forms exactly the same character. It may be that there is a kind of biological isomerism, in which, instead of molecules of the same formula having different physical properties, there are isomers capable of forming the same character, although, through difference in construction, they are not allelomorphic to each other. At least it is quite a probable supposition that through imperfections in the mechanism of heredity an individual possessing a certain character

should give rise to different lines of descent so that in the  $F_n$  generation when individuals of these different lines are crossed, the character behaves as a di-hybrid instead of as a mono-hybrid. In other words, it is more probable that these units arise through variation in different individuals and are combined by hybridization, than that actually different structures for forming the same character arise in the same individual.

On the other hand, there is a possibility of an action just the opposite of this. Several of these quantitative units which produce the same character may become attached like a chemical radical and again behave as a single pair. Nilsson-Ehle gives one case which he does not attempt to explain, where the same cross gave a 4:1 ratio in one instance and 8.4:1 ratio in another instance. In his other work characters always behaved the same way; that is, either as one pair, two pairs, three pairs, etc. In my work, the yellow endosperm of maize has behaved differently in the same strain, but it is probably because the yellow parent is homozygous for one yellow and heterozygous for the other. They were known to be pure for one yellow, but it would take a long series of crosses to prove purity in two yellows.

Let us now consider what is the concrete result of the inter-action of several cumulative units affecting the same character. Where there is simple presence dominant to absence of a number  $n$  of such factors, in a cross where all are present in one parent and all absent in the other parent, there must be  $4^n$  individuals to run an even chance of obtaining a single  $F_2$  individual in which the character is absent. When four such units,  $A_1A_2A_3A_4$  are crossed with  $a_1a_2a_3a_4$ , their absence, only one pure recessive is expected in 256 individuals. And 256 individuals is a larger number than is usually reported in genetic publications. When a smaller population is considered, it will appear to be a blend of the two parents with a fluctuating variability on each side of its mode. Of course if there is absolute dominance and each unit appears to affect the

zygote in the same manner that they do when combined, the  $F_2$  generation will appear like the dominant parent unless a very large number of progeny are under observation and pure recessives are obtained. This may be an explanation of the results obtained by Millardet; it is certainly as probable as the hypothesis of the non-formation of homozygotes. Ordinarily, however, there is not perfect dominance, and variation due to heterozygosis combined with fluctuating variation makes it almost impossible to classify the individuals except by breeding. The two yellows in the endosperm of maize is an example of how few characters are necessary to make classification difficult. First, there is a small amount of fluctuation in different ears due to varying light conditions owing to differences in thickness of the husk; second, all the classes having different gametic formulæ differ in the intensity of their yellow in the following order,  $Y_1Y_1Y_2Y_2$ ,  $Y_1y_1Y_2Y_2$  or  $Y_1Y_1Y_2y_2$ ,  $Y_1Y_1$ ,  $Y_2Y_2$ ,  $Y_1y_1$ ,  $Y_2y_2$ ,  $y_1y_2$ . As dominance becomes less and less evident, the Mendelian classes vary more and more from the formula  $(3+1)^n$ , and approach the normal curve, with a regular gradation of individuals on each side of the mode. When there is no dominance and open fertilization, a state is reached in which the curve of variation simulates the fluctuation curve, with the difference that the gradations are heritable.

One other important feature of this class of genetic facts must be considered. If units  $A_1A_2A_3a_4$  meet units  $a_1a_2a_3A_4$ , in the  $F_2$  generation there will be one pure recessive,  $a_1a_2a_3a_4$ , in every 256 individuals. This explains an apparent paradox. Two individuals are crossed, both seemingly pure for presence of the same character, yet one individual out of 256 is a pure recessive. When we consider the rarity with which pure dominants or pure recessives (for all characters) are obtained when there are more than three factors, we can hardly avoid the suspicion that here is a perfectly logical way of accounting for many cases of so-called atavism. Furthermore, many ap-

parently new characters may be formed by the gradual dropping of these cumulative factors without any additional hypothesis. For example, in *Nicotiana tabacum* varieties there is every gradation<sup>6</sup> of loss of leaf surface near the base of the sessile leaf, until in *N. tabacum fruticosa* the leaf is only one step removed from a petioled condition. If this step should occur the new plant would almost certainly be called a new species; yet it is only one degree further in a definite series of loss gradations that have already taken place. If it should be assumed that in other instances slight qualitative as well as quantitative changes take place as units are added, then it becomes very easy, theoretically, to account for quite different characters in the individual homozygous for presence of all dominant units, and in the individual in which they are all absent.

Unfortunately for these conceptions, although I feel it extremely probable that variations in *some* characters that seem to be continuous will prove to be combinations of segregating characters, it is exceedingly difficult to demonstrate the matter beyond a reasonable doubt. As an illustration of the difficulties involved in the analysis of pedigree cultures embracing such characters, I wish to discuss some data regarding the inheritance of the number of rows of kernels on the maize cob.

The maize ear may be regarded as a fusion of four or more spikes, each joint of the rachis bearing two spikelets. The rows are, therefore, distinctly paired, and no case is known where one of the pair has been aborted. This is a peculiar fact when we consider the great number of odd kinds of variations that occur in nature. The number of rows per cob has been considered to belong to continuous variations by DeVries, and a glance at the progeny from the seeds of a single selfed ear as shown in Table V seems to confirm this view.

There is considerable evidence, however, that this character is made up of a series of cumulative units, inde-

<sup>6</sup> It is not known at present how this character behaves in inheritance.

TABLE V.

PROGENY OF A SELFED EAR OF LEAMING MAIZE HAVING 20 ROWS

Classes of rows.....	12	14	16	18	20	22	24	26	28	30
No. of ears. ....	1	0	5	4	53	35	19	5	2	1

pendent in their inheritance. There is no reason why it should not be considered to be of the same nature as various other size characters in which variation seems to be continuous, but in which relatively constant gradations may be isolated, each fluctuating around a particular mode. But this particular case possesses an advantage not held by most phenomena of its class, in that there is a definite discontinuous series of numbers by which each individual may be classified.

Previous to analyzing the data from pedigree cultures, however, it is necessary to take into consideration several facts. In the first place, what limits are to be placed on fluctuations?<sup>7</sup> From the variability of the progeny of single ears of dent varieties that have been inbred for several generations, it might be concluded that the deviations are very large. But this is not necessarily the case; these deviations may be due largely to gametic structure in spite of the inbreeding, since no conscious selection of homozygotes has been made. There is no such variation in eight-rowed varieties, which may be considered as the last subtraction form in which maize appears and therefore an extreme homozygous recessive. In a count of the population of an isolated maize field where Longfellow, an eight-rowed flint, had been grown for many years, 4 four-rowed, 993 eight-rowed, 2 ten-rowed and 1 twelve-rowed ears were found. Only seven aberrant ears out of a thousand had been produced, and some of these may have been due to vicinism.

On the other hand a large number of counts of the number of rows of both ears on stalks that bore two ears has shown that it is very rare that there is a change

<sup>7</sup> The word fluctuation is used to designate the somatic changes due to immediate environment, and which *are not inherited*.

greater than  $\pm 2$  rows. If conditions are more favorable at the time when the upper ear is laid down it will have two more rows than the second ear; if conditions are favorable all through the season, the ears generally have the same number of rows; while if conditions are unfavorable when the upper ear is laid down, the lower ear may have two more rows than the upper ear. Furthermore, seeds from the same ear have several times been grown on different soils and in different seasons, and in each case the frequency distribution has been the same. Hence it may be concluded that in the great majority of cases fluctuation is not greater than in  $\pm 2$  rows, although fluctuations of  $\pm 4$  rows have been found.

A second question worthy of consideration is: Do somatic variations due to varying conditions during development take place with equal frequency in individuals with a large number of rows and in individuals with a small number of rows? From the fact that several of my inbred strains that have been selected for three generations for a constant number of rows, increase directly in variability as the number of rows increases, the question should probably be answered in the negative. This answer is reasonable upon other grounds. The eight-rowed ear may vary in any one of four spikes, the sixteen-rowed ear may vary in any one of eight spikes; therefore the sixteen-rowed ear may vary twice as often as the eight-rowed ear. By the same reasoning, the sixteen-rowed ear may sometimes throw fluctuations twice as wide as the eight-rowed ear.

A third consideration is the possibility of increased fluctuation due to hybridization. Shull<sup>8</sup> and East<sup>9</sup> have shown that there is an increased stimulus to cell division when maize biotypes are crossed—a phenomenon apart from inheritance. There is no evidence, however, that

<sup>8</sup> Shull, G. H., "A Pure-line Method in Corn Breeding," *Rept. Amer. Breeders' Assn.*, 5, 51-59, 1909.

<sup>9</sup> East, E. M., "The Distinction between Development and Heredity in Inbreeding," *AMER. NAT.*, 43, 173-181, 1909.

increased gametic variability results. Johannsen<sup>10</sup> has shown that there is no such increase in fluctuation when close-pollinated plants are crossed. I have crossed several distinct varieties of maize where the modal number of rows of each parent was twelve, and in every instance the  $F_1$  progeny had the same mode and about the same variability.

Finally, a possibility of gametic coupling should be considered. Our common races of flint maize all have a low number of rows, usually eight but sometimes twelve; dent races have various modes running from twelve to twenty-four rows. When crosses between the two subspecies are made, the tendency is to separate in the same manner.

Attention is not called to these obscuring factors with the idea that they are universally applicable in the study of supposed continuous variation. But there are similar conditions always present that make analysis of these variations difficult, and the facts given here should serve to prevent premature decision that they do not show segregation in their inheritance.

Table VI shows the results from several crosses between maize races with different modal values for number of rows. Several interesting points are noticeable. The modal number is always divisible by four. This is also the case with some twenty-five other races that I have examined but which are not shown in the table. I suspect that through the presence of pure units zygotes having a multiple of four rows are formed, while heterozygous units cause the dropping of two rows. The eight-rowed races are pure for that character, the twelve-rowed races vary but little, but the races having a higher number of rows are exceedingly variable.

When twelve-rowed races are crossed with those having eight rows, the resulting  $F_1$  generation always—or nearly

<sup>10</sup> Johannsen, W., "Does Hybridization Increase Fluctuating Variability?" *Rept. Third Inter. Con. on Genetics*, 98–113, London, Spottiswoode, 1907.

TABLE VI.

CROSSES BETWEEN MAIZE STRAINS WITH DIFFERENT NUMBERS OF ROWS

Parents. (Female Given First.)	Gen.	Row Classes.						
		8	10	12	14	16	18	20
Flint No. 5.....		100						
Flint No. 11.....		1	4	387	7	1		
Flint No. 24.....		100						
Flint No. 15.....		100						
Dent No. 6.....				6	31	51	18	4
Dent No. 8.....			3	54	36	12	2	
Sweet No. 53 <sup>11</sup> .....		1	5	25	4			
Sweet No. 54 <sup>11</sup> .....		25	2	1				
No. 5 × No. 53.....	$F_1$	1	7	13				
No. 5 × No. 6.....	$F_1$	11	18	27	3			
No. 11 × No. 5.....	$F_1$	2	4	18				
No. 11 × No. 53.....	$F_1$	2	5	17				
No. 24 × No. 53.....	$F_1$	57	8	3				
No. 15 × No. 8.....	$F_1$	1	14	26	3	1		
No. 15 × No. 8 (from 10-row ear)..<	$F_2$	14	15	28	9	1		
No. 15 × No. 8 (from 12-row ear)..<	$F_2$	4	13	25	6	3		
No. 8 × No. 54.....	$F_1$	1	6	14				
No. 8 × No. 54 (from 12-row ear)..<	$F_2$	11	25	38	2	1		

always—has the mode at twelve rows. In one case cited in Table VI, No. 24 × No. 53, nearly all the  $F_1$  progeny were eight-rowed. It might appear from this, either that the low number of rows was in this case dominant, or that the female parent has more influence on the resulting progeny than the male parent. I prefer to believe, however, that the individual of No. 53 which furnished the pollen was due to produce eight-rowed progeny. Unfortunately no record was kept of the ear borne by this plant, but No. 53 sometimes does produce eight-rowed ears.

When a race with a mode higher than twelve is crossed with an eight-rowed race, the  $F_1$  generation is always intermediate, although it tends to be nearer the high-rowed parent. Only one example is given in the table, but it is indicative of the class. These results are rather confusing, for there seems to be a tendency to dominance in the twelve-rowed form that is not found in the forms with a higher number of rows. I have seen cultures of other investigators where 12-row × 8-row resulted in a

<sup>11</sup> Approximately.

ten-rowed  $F_1$  generation, so the complication need not worry us at present.

The results of the  $F_2$  generation show a definite tendency toward segregation and reproduction of the parent types. I might add that in at least two cases I have planted extracted eight-rowed ears and have immediately obtained an eight-rowed race which showed only slight departures from the type. Selection from those ears having a high number of rows has also given races like the high-rowed parent without recrossing with it. It is regretted that commercial problems were on hand at the time and no exact data were recorded. It can be stated with confidence, however, that ears like each parent are obtained in the  $F_2$  generation, from which with care *races* like each parent may be produced. *Segregation seems to be the best interpretation of the matter.*

These various items may seem disconnected and uninteresting, but they have been given to show the tangible basis for the following theoretical interpretation. No hard and fast conclusion is attempted, but I feel that this interpretation with possibly slight modifications will be found to aid the explanation of many cases where variation is apparently continuous.

Suppose a basal unit to be present in the gametes of all maize races, this unit to account for the production of eight rows. Let additional independent interchangeable units, each allelomorphic to its own absence, account for each additional four rows; and let the heterozygous condition of any unit represent only half of the homozygous condition, or two rows. Then the gametic condition of a homozygous twenty-rowed race would be  $8 + AAB BCC$ , each letter actually representing two rows. When crossed with an eight-rowed race, the  $F_2$  generation will show ears of from eight to twenty rows, each class being represented by the number of units in the coefficients in the binomial expansion where the exponent is twice the number of characters, or in this case  $(a + b)^6$ .

The result appears to be a blend between the characters

of the two parents with a normal frequency distribution of the deviants. Only one twenty-rowed individual occurs in 64 instead of the 27 expected by the interaction of three dominant factors in the usual Mendelian ratios. The remainder of the 27 will have different numbers of rows, and, by their gametic formulæ, different expectations in future breeding as follows:

- 1  $AAB\bar{B}CC = 20$  rows.
- 2  $AaBBCC = 18$  rows.
- 2  $AABbCC = 18$  rows.
- 2  $AABBCc = 18$  rows.
- 4  $AaBbCC = 16$  rows.
- 4  $AaBBCc = 16$  rows.
- 4  $AABbCc = 16$  rows.
- 8  $AaBbCc = 14$  rows.

There are four visibly different classes and eight gametically different classes. It must also be remembered that the probability that the original twenty-rowed ear in actual practise may have had more than three units in its gametes has not been considered. This point is illustrated clearly if we work out the complete ratio for the three characters, and note the number of gametically different classes which compose the modal class of fourteen

TABLE VII

THEORETICAL EXPECTATION IN  $F_2$  WHEN A HOMOZYGOUS TWENTY-ROWED MAIZE EAR IS CROSSED WITH AN EIGHT-ROWED EAR

Classes.....	8	10	12	14	16	18	20
No. ears.....	1	6	15	20	15	6	1

rows in Table VII. It actually contains seven gametically different classes and not a single homozygote. If this conception of independent allelomorphic pairs affecting the same character proves true, it will sadly upset the biometric belief that the modal class is *the type* around which the variants converge, for there is actually less chance of these individuals breeding true than those from *any other* class.

The conception is simple and is capable theoretically of bringing in order many complicated facts, although the presence of fluctuating variation will be a great factor in preventing analysis of data. I have thought of only one fact that is difficult to bring into line. If *8AA*, *8BB* and *8CC* all represent homozygous twelve-rowed ears—to continue the maize illustration—and none of these factors are allelomorphous to each other, sixteen-rowed ears should sometimes be obtained when crossing two twelve-rowed ears. I am not sure but that this would happen if we were to extract all the homozygous twelve-rowed strains after a cross between sixteen-row and eight-row, and after proving their purity cross them. In some cases the additional four-row units would probably be allelomorphous to each other and in other cases independent of each other. On the other hand, this is only an hypothesis, and while I have faith in its foundation facts, the details may need change.

Castle has raised the point that greater variation should be expected in the  $F_1$  generation than in the  $P_1$  generations when crossing widely deviating individuals showing variation apparently continuous. If the parents are strictly pure for a definite number of units, say for size, a greater variation should certainly be expected in the  $F_1$  generation after crossing. But considering the difficulties that arise when even five independent units are considered, can it be said that anything has heretofore been known concerning the actual gametic status of parents which it is known do vary in the character in question and in which the variations are inherited, for the race can be changed by selection within it. It may be, too, that the correct criterion has not been used in size measurements, for, as others have suggested, solids vary as the cube root of their mass, whereas the sum of the weights of the body cells has usually been measured and compared directly with similar sums.

Attention should be called to one further point. Many characters in all probability are truly blending in their

inheritance, but there is another interpretation which may apply in certain cases. I have repeatedly tried to cross Giant Missouri Cob Pipe maize (14 feet high) and Tom Thumb pop maize (2 feet high), but have always failed. They both cross readily with varieties intermediate in size, but are sterile between themselves. We may imagine that the gametes of each race, though varying in structure, are all so dissimilar that none of them can unite to form zygotes. Other races may be found where only part of the gametes of varying structure are so unlike that they will not develop after fusion. The zygotes that do develop will be from those more alike in construction. An apparent blend results, and although segregation may take place, no progeny as extreme as either of the parents will ever occur.

I may say in conclusion that the effect of the truth of this hypothesis would be to add another link to the increasing chain of evidence that the word mutation may properly be applied to any inherited variation, however small; and the word fluctuation should be restricted to those variations due to immediate environment which do not affect the germ cells, and which—it has been shown—are not inherited. In addition it gives a rational basis for the origin of *new* characters, which has hitherto been somewhat of a Mendelian stumbling-block; and also gives the term unit-character less of an irrevocably-fixed-entity conception, which is more in accord with other biological beliefs.